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# TAXONOMY OF *PRIMULA* SECTS. *ALEURITIA* AND *ARMERINA* IN NORTH AMERICA

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## ABSTRACT

In North America the genus *Primula* has several representatives in section *Aleuritia* Duby and section *Armerina* Lindley. These sections were originally treated as related subsections in the large section *Farinosae* Pax. Their members have been the subject of much misinterpretation, particularly in arctic and boreal North America where few collections and no modern systematic treatment existed. North American members of these two sections are reviewed here with particular attention to the arctic and boreal taxa. Section *Aleuritia* ($x = 9$) is represented by 4 diploid species: *P. alcalina, P. anvilensis, P. mistassinica,* and *P. specuicola,* and 4 polyploid species: *P. borealis* ($4x$), *P. incana* ($6x$), *P. laurentiana* ($8x$), and *P. stricta* ($14x$). Section *Armerina* ($x = 11$) is represented by a diploid species, *P. nutans* (formerly *P. sibirica*), and a tetraploid species, *P. egaliksensis.*

Key Words: Primulaceae, *Primula* sect. *Aleuritia, Primula* sect. *Armerina, Primula* sect. *Farinosae,* taxonomy, phytogeography, Arctic, North America

## INTRODUCTION

The large genus *Primula* L. (Primulaceae) is widely distributed throughout the northern latitudes of Eurasia and North America. Of ca. 500 species now recognized, the majority are found in the mountains of Asia. In North America, there are approximately twenty-five species representing five sections of the genus. Of these, members of sect. *Armerina* Lindley and sect. *Aleuritia* Duby have been especially subject to taxonomic confusion due to their morphological and ecological similarity, and to their distribution in remote northern areas where field studies have been limited or nonexistent.

This paper provides a comprehensive taxonomic treatment of sections *Aleuritia* and *Armerina* in North America with special attention given to poorly understood arctic and boreal taxa. It is appropriate to discuss these sections together for several reasons. They were initially treated (Bruun, 1932; Smith and Fletcher, 1943) as closely related subsections in a section then called *Farinosae* Pax. Many of the taxa superficially resemble one another and some grow sympatrically. Analyses by Wendelbo (1961) and Schwarz (1968) have showed some fundamental differences between these sections in Eurasia, but until now the North American taxa have not been examined. This study supports recognition of two distinct sections on the basis of cytology, anatomy, and morphology. There are eight members of section *Aleuritia* in North America (*Primula alcalina* Cholewa & Henderson, *P. anvilensis* Kelso, *P. borealis* Duby, *P. incana* M. E. Jones, *P. laurentiana* Fernald, *P. mistassinica* Michaux, *P. specuicola* Fernald, and *P. stricta* Hornemann) and two members of section *Armerina* (*P. egaliksensis* Wormskjold and *P. nutans* Georgi, formerly *P. sibirica* Jacq.).

## TAXONOMIC HISTORY

Monographic treatments of *Primula* were done by Lehmann (1817), Duby (1844), Pax (1889, 1890), Pax and Knuth (1905), and Smith and Fletcher (1943). Although the work of Smith and Fletcher was based on morphological interpretations of taxa and limited material of some species, it stands as the most comprehensive taxonomic treatment of the genus to date.

Infrageneric arrangement of *Primula* by Duby (1844) was based on gross morphology without regard to the more phylogenetically relevant characters in cytology, anatomy, or chemistry seen as essential in contemporary systematics. This arrangement was revised by Balfour (1913), Bruun (1932), Smith and Forrest (1928), and Wendelbo (1961), with additional modification by Schwarz (1968).

No comprehensive examination of the North American primulas has been carried out to date. Fernald (1928) revised section *Farinosae* and Williams (1936) provided a brief overview of the genus in western North America. Since these papers were published, several new taxa have been described, the descriptions of others have been modified, and considerably more has been learned about the ecology and biogeography of the genus in North America.

## MATERIALS AND METHODS

Field studies were carried out in Alaska at numerous locations from the Seward Peninsula, the Alaska Range around Denali National Park, along the Tanana River in Fairbanks, the Delta River near Donnelly Creek, and the Northway region along the upper Tanana River. In the Yukon, populations were studied along the Donjek River, the confluence of the White and Koidern Rivers, and from Kluane Lake. In addition, live material from various arctic regions was cultivated in gardens in Fairbanks.

Morphological characteristics of approximately 1300 herbarium specimens from ALA, ALTA, BM, BRY, CAN, CAS, COLO, DAO, E, GH, ID, ISC, K, NDG, NY, PH, RS, S, T, UBC, UPS, US, UTC, and WTU were examined. These specimens represented *Primula* taxa over their entire range.

Chromosome numbers reported here are original counts or are referenced as literature reports. Methodology for the cytological and anatomical analysis and complete lists of specimens examined are given in Kelso (Ph.D. dissertation, Univ. of Alaska, Fairbanks, 1987).

## TAXONOMIC CHARACTERS IN *PRIMULA*

Although large and geographically widespread, *Primula* is not a morphologically diverse genus. Species of *Primula,* and likewise genera in the Primulaceae, are often distinguished by a combination of characters rather than by a single attribute. These diagnostic attributes can change with ontogeny. For example, height of the scape can increase six-fold during blooming, farina that is dense on young leaves almost disappears on individuals in fruit, arching pedicels at anthesis stiffen and become erect as capsules ripen. Furthermore, individuals are often phenotypically plastic in their vegetative and reproductive responses to environmental conditions. However, while it is necessary in northern species of *Primula* to allow for generous morphological amplitude according to the effects of phenology and environment, all taxa discussed here show a coherent and identifiable phenotype.

It is critical to recognize the importance of reproductive biology in the taxonomy, ecology, and evolution of *Primula.* While *Primula* has long been known for its high incidence of distyly (Darwin, 1889), and a considerable amount is known about the genetic basis for this complex reproductive, morphological, and biochemical system (see, among others, Ganders, 1979; Charlesworth and Charlesworth, 1979; Richards, 1986), little attention has been paid to distyly and homostyly as taxonomic characters or to their evolutionary significance in related species. Due to the strong intramorph incompatibility reaction, distylous individuals are virtually obligate outcrossers, while homostylous individuals are self-fertile and probably highly autogamous due to the proximity of the reproductive organs.

In the two sections treated here, there are both distylous and homostylous taxa. Distyly and homostyly are reliable taxonomic markers: in several thousand individuals examined during this study, taxa were either completely distylous or completely homostylous. Contrary to the misconception that arctic plants must have facultative selfing capacity to cope with a short growing season, several arctic species of *Primula* are distylous with concomitant obligate outcrossing. Other arctic primulas, often widespread polyploids, are homostylous and self-fertile.

To some extent, homostyly and polyploidy are linked in *Primula.* Diploid species tend to be distylous, tetraploids can be distylous or homostylous, and higher polyploids are all homostylous. *Primula* section *Aleuritia,* with a base number of $x = 9$, contains taxa ranging from $2x$ to $14x$. Although chromosome reports in the literature suggest that some species have several chromosome races, almost all cases can be shown to be the result of faulty determination of the taxa examined. Section *Armerina* ($x = 11$) contains a distylous diploid species and a homostylous tetraploid one. Chromosome number is thus a very strong taxonomic character in at least these two sections of *Primula,* both on an intersectional and an interspecific basis.

The chemical nature of the powdery exudate known as "farina" that is common in some species of *Primula* has been of interest to a number of authors (Blasdale, 1945, 1947; Harborne, 1968; Wollenweber, 1974; Sellmair et al., 1977). While all species appear to have at least a few relictually farinipotent glands, glandular development is most pronounced on species with abundant farina. The farina is composed primarily of flavones of varying chemical composition (Harborne, 1971), but it is not clear that the chemical composition has systematic significance or whether farina composition remains constant throughout a species, throughout a population, or throughout a growing season. The common occurrence of efarinose individuals or populations in normally farinose species, and the dramatic drop in farina production on farinose individuals toward the end of the growing season indicates that it is unwise to rely heavily on this character.

At the anatomical level, sections and sometimes species, can be distinguished by the glands and pollen grains. All species of *Primula* have either articulated hairs or glands on at least some of their vegetative parts. Members of section *Aleuritia,* where farina is common, have glands with a large apical cell and one to three smaller basal cells, while members of section *Armerina,* all of which are efarinose, have articulated hairs. *Primula egaliksensis,* although efarinose, also contains a few glands similar to those in section *Aleuritia.* While pollen grains have been used as taxonomic and phylogenetic markers at the generic level in the Primulaceae (Wendelbo, 1961; Nowicke and Skvarla, 1977), until now little attention has been given to a comparative study of pollen morphology at the subgeneric level, or to the effects of polyploidy on that morphology.

Exine ornamentation can be diagnostic at the sectional level for North American primulas. The number of colpi per pollen grain correlates with polyploidy and can thus be a useful character at the species level. Members of section *Aleuritia,* for example, have microreticulate exine, with diploids and tetraploids having tricolpate grains. Both the hexaploid *Primula incana* and the octoploid *P. laurentiana* have 4-colpate grains, and the decatetraploid *P. stricta* has 5-colpate grains. In section *Armerina, P. nutans* shows the broadly reticulate exine and 6-stephanocolpate pollen that is typical of Eurasiatic members (Nasir, 1987).

The most useful characters for identifying species in sections *Armerina* and *Aleuritia* are certain aspects of floral and vegetative morphology. The following features are important:

1. LEAF SHAPE. Members of section *Armerina* are strongly petiolate, with a thin, efarinose, oval or elliptical blade with entire margins. Members of section *Aleuritia* have spathulate leaves that are often farinose and denticulate on the upper margins. Because most primulas bloom early, their leaves are not fully expanded at anthesis. Enlargement occurs over the growing season, and by the time capsules are ripe, leaves may be up to four times their size at early anthesis. In addition, vegetative growth in *Primula* is responsive to nutrient availability, and luxuriant forms can be seen in protected or nutrient-rich areas such as in sites with resident bird populations. These forms are particularly dramatic in normally dwarf tundra species, and led to some of the early taxonomic confusion when authors described taxa based on few specimens and no field experience.

2. Bracts. All species of *Primula* have several involucral bracts subtending the umbel. The shape at the tip (involute or flat), the shape at the base (flat or saccate), and the presence or absence of auricles of these bracts can be useful at both the sectional and the specific level.

3. Height. Scape height is most reliable as a taxonomic marker when measured at full (when most of the flowers in the umbel are in bloom) or late anthesis. Several arctic species begin blooming early when plants are virtually ascapose. Elongation of the scape continues throughout anthesis until the capsules are ripe, and the fruiting plant can be several times as tall as the plant in first bloom. The increase is most noticeable in the taller species like *P. incana* or *P. laurentiana* which are frequently misidentified as their shorter relatives *P. stricta* and *P. mistassinica,* respectively.

4. Pedicels. As capsules ripen and elongation of the scape slows and eventually ceases, elongation and stiffening of the pedicels occurs. At anthesis, the length and posture of pedicels are both strong taxonomic markers at the species level. In fruit, however, the shape of the umbel is very different, and neither length nor posture of the pedicels is a reliable character for distinguishing between species.

5. Flower Number. The number of flowers per umbel of any individual plant is to a certain extent species specific, but it can also be influenced by length of the growing season. Individuals with multi-flowered umbels bloom asynchronously, and those plants that emerge early from snow cover have a longer season in which to develop flowers than those blooming later.

6. Calyx. Significant differences in the shape and degree to which the calyx is divided are diagnostic at the sectional level. In both sections examined here, the calyx bears lanceolate teeth. In sect. *Armerina,* it is cylindrical, ribless, and divided less than one quarter of its length. In comparison, members of section *Aleuritia* have a campanulate obscurely ribbed calyx that is divided one third to one half its length. Calyx size in *Primula* is generally

correlated with overall size of the individual plant and is not a useful character.

7. COROLLA. The length of the corolla tube relative to the calyx can be diagnostic at the species level. This is consistent during the period of anthesis; however, in all taxa the tube elongates rapidly between the bud stage and time of flower opening. Relative sizes can be measured accurately only when flowers are in full bloom.

Corolla size, as measured by width across the limb, can also be a useful character at the species level. To a certain extent, flower size is correlated with the breeding system: pollinator-dependent distylous species tend to have larger flowers than self-fertile homostyles.

Two species in section *Aleuritia* (*Primula alcalina* and *P. anvilensis*) have consistently white flowers. Other species in both sections *Aleuritia* and *Armerina* have lavender flowers, although *P. egaliksensis* has equally abundant white and lavender forms, and *P. mistassinica* has a white form common in Newfoundland. Flower color is deepest in young flowers, and gradually fades with maturity. Herbarium specimens can be deceptive since drying causes many lavender flowers to fade and appear white.

8. CAPSULES. Capsule shape follows sectional lines. Members of section *Aleuritia* have elliptical to broadly cylindrical capsules, while members of section *Armerina* have narrowly cylindrical capsules. With the exception of *Primula stricta* which has characteristic short capsules, it is difficult to distinguish the capsules of related species. Fruiting specimens of *Primula* are the most difficult to identify on the basis of morphology alone, and for these individuals, anatomical and/or ecological features may be helpful.

9. ECOLOGY. All North American species of *Primula* show a preference for cool, moist, open habitats disturbed by frost action, flooding, or downslope movement. Members of section *Aleuritia* show a strong affinity for alkaline soils. Among these, *P. borealis* is confined to salt marshes, *P. incana* to inland clay soils, and *P. specuicola* to canyon walls. Other members, particularly the widespread *P. mistassinica,* have less specific habitat requirements, and can be found on lake shores, along stream beds or roadsides,

or around hot springs. In section *Armerina, P. nutans* on the west coast of Alaska is restricted to salt marshes, but in the interior of the state and in the Yukon it is found in freshwater marshes.

## EVOLUTIONARY HISTORY

SECT. *Aleuritia.* The polyploid complex in sect. *Aleuritia* can be explained by the secondary contact model described by Stebbins (1950, 1985). In this model, an initially widespread taxon is fragmented into disjunct populations by a catastrophic event such as climate change, but these gene pools do not differentiate enough for complete reproductive isolation. If the ecological or geological barriers are removed, taxa can come into secondary contact forming a complex pattern of allopolyploid hybrids. The success of these polyploids is promoted by the availability of new open habitats. I suggest this model may be applicable for sect. *Aleuritia* as follows:

Prior to the late Quaternary glaciation, a diploid similar to *Primula mistassinica* was widespread across North America in the boreal regions. At this time Alaska was isolated by the confluence of the Cordilleran and Laurentide ice, and a remnant of this diploid remained there in the Bering Strait region as *P. anvilensis* of today. South of the ice sheets, there was further fragmentation of the ancestral diploid. Vogelmann (Ph.D. dissertation, Univ. of Michigan, 1956) has suggested that *P. mistassinica* survived Pleistocene glaciation in separate refugia, including Newfoundland, the Appalachians, and the Midwest. It seems likely that the narrow endemics *P. alcalina* in Idaho and *P. specuicola* in the Southwest were completely isolated and adapted *in situ* to the local conditions as the climate became warmer and drier in postglacial times. In contrast, the eastern populations of *P. mistassinica* rejoined as they migrated north following glacial retreat, and now show only infraspecific variation as local races.

The concatenation of eastern populations provided the basis for a polyploid complex. The hexaploid *Primula incana* and the octoploid *P. laurentiana* can be seen as the result of hybridization between the partially differentiated diploid populations. As self-fertile homostyles, these polyploids were able to become established and spread rapidly into the deglaciated regions where they are found today.

In Europe there is a parallel situation with the diploid species *Primula farinosa* L., the hexaploid *P. scotica* Hook. and the octoploid *P. scandinavica* Bruun. Like *P. mistassinica, P. farinosa* probably survived glaciation in several refugia and these populations rejoined to form allopolyploids. The amphi-Atlantic species *P. stricta,* a 14-ploid, may be a hybrid between *P. scotica* and *P. scandinavica* as suggested by Knaben (1982), but the North American *P. incana* and *P. laurentiana* are equally probable progenitors. The contemporary distribution of *P. stricta* is not convincing evidence for postglacial migration in either direction. Its range is larger in North America than in Europe, but this may only be due to more suitable habitat in the Canadian Arctic Archipelago. The heritage of *P. stricta* remains an open question until further genetic evidence can be obtained.

The origin of the tetraploid *Primula borealis* of the Bering Sea coast is somewhat problematic as well. It has a close morphological affinity with the Japanese species *P. modesta* Bisset & Moore *s. lat.*, and on biogeographic grounds it is reasonable to suggest that *P. borealis* is a recent tetraploid derivative of the Asian *P. farinosa–P. modesta* complex rather than of the North American *P. mistassinica* line.

SECT. *Armerina.* On the basis of morphology, anatomy, and cytology, members of this primarily Asiatic section are distinguishable from those belonging to sect. *Aleuritia,* and recognition of these as phylogenetically separate is clearly justified. The wide distribution of *Primula nutans* across Eurasia suggests that it is an old taxon. Mäkinen and Mäkinen (1964) have described how Pleistocene isolation may have resulted in the Fennoscandian subspecies *finnmarchia,* which differs only in a short corolla tube. The scattered populations of *P. nutans* found in North America are probably Pleistocene survivors that persisted in unglaciated Alaska and the Yukon. If *P. nutans* once extended further east, it must have been extirpated there by the late glacial ice sheets.

*Primula egaliksensis* is a homostylous tetraploid with such a strong resemblance to *P. nutans* that Fernald (1928) and Smith and Fletcher (1943) assumed it was a derivative of that species without knowing the cytological status of the two. As for the polyploids in sect. *Aleuritia,* a change in the breeding system from distyly to homostyly brought self-fertility and the potential for colonizing recently deglaciated habitats. Today *P. egaliksensis* is widespread across North America from Alaska to Newfoundland in areas that were covered by ice until the late Pleistocene.

## TAXONOMIC TREATMENT

### KEY TO THE SECTIONS OF *PRIMULA* IN NORTH AMERICA

1. Leaves broadly dentate at the apex, capsules globose, seeds with flanged edges . . . . . . . . . . . . . . . . . . . . . sect. *Cuneifolia*
1. Plants not as above . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 2
    2. Corolla lobes entire . . . . . . . . . . . . . sect. *Crystallophlomis*
    2. Corolla lobes cleft or notched . . . . . . . . . . . . . . . . . . . . . . 3
        3. Flowers magenta pink, often glandular at base of corolla tube, leaves lanceolate to broadly spathulate, capsules broadly cylindrical, rarely ovate . . . . . . sect. *Parryi*
        3. Flowers lavender pink or white, eglandular, leaves spathulate to ovate, capsules elliptical or narrowly cylindrical . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 4
            4. Leaves distinctly petiolate, blades ovate or elliptical, plants efarinose, capsules narrowly cylindrical . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . sect. *Armerina*
            4. Leaves indistinctly petiolate to spathulate, plants usually farinose, rarely efarinose, capsules elliptical to ovate . . . . . . . . . . . . . . . . . . . . sect. *Aleuritia*

### **Primula** sect. **Aleuritia**

**Primula** sect. **Aleuritia** Duby, in DeCandolle, Prodromus 8: 41. 1844.—*pro parte.* Emend. Wendelbo, Aarbok Univ. Bergen, Mat.-Naturvitensk. Ser. 1961: 37. 1961. TYPE: *P. farinosa* L.

Section *Farinosae* Pax, Bot. Jahrb. Syst. 10: 194. 1889.—*pro parte.*

Plants usually farinose or with farinipotent glands, lacking rhizomes. Leaves with revolute vernation, blades decurrent, lanceolate to spathulate, glabrous. Inflorescence a simple umbel subtended by involucral bracts usually saccate or gibbous at base, rarely plane; pedicels usually erect, sometimes flexuous. Corolla lilac, pink, or white; lobes notched or cleft. Capsules elliptical to broadly ovate. Chromosome base number: $x = 9$.

### KEY TO SECTION *ALEURITIA*

1. Flowers distylous . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 2
    2. Involucral bracts saccate or gibbous at base; plants of coastal salt marshes . . . . . . . . . . . . . . . . . . . . . . . . . *P. borealis*
    2. Involucral bracts plane at base; plants not of coastal salt marshes . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 3
        3. Corolla limb always white . . . . . . . . . . . . . . . . . . . . . . . 4
            4. Plants farinose; pedicels erect at anthesis, shorter than bracts . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. alcalina*
            4. Plants efarinose; pedicels arching at anthesis, longer than bracts . . . . . . . . . . . . . . . . . . . . *P. anvilensis*
        3. Corolla limb lavender, rarely white . . . . . . . . . . . . . . 5
            5. Leaves heavily white farinose . . . . . . . *P. specuicola*
            5. Leaves yellow farinose or efarinose . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. mistassinica*
1. Plants homostylous . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 6
    6. Corolla limb 8–16 mm in diameter, leaf margins distinctly crenate . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. laurentiana*
    6. Corolla limb 4–8 mm in diameter, leaf margins entire to denticulate at apex only . . . . . . . . . . . . . . . . . . . . . . . . 7
        7. Leaves and calyces slightly farinose; capsules ovate, only slightly longer than the calyx . . . . . . . . . . . *P. stricta*
        7. Leaves and calyces heavily farinose; capsules elliptical and strongly exserted from the calyx . . . . *P. incana*

**Primula alcalina** A. Cholewa & D. Henderson, Brittonia 36: 59–62. 1984. Figure 1A. TYPE: U.S.A. IDAHO. Lemhi Co., 10 mi. north of Blue Dome along Birch Creek, *Henderson and Cates 1372* (HOLOTYPE: ID; ISOTYPE: NY!).

Plants farinose only when young, efarinose in age. Scape 6.5–24 cm high. Leaves elliptic-oblanceolate, blade narrowing gradually onto winged petiole, 1–4 cm long, margins crenulate or denticulate, sometimes entire. Involucral bracts plane at base, .4–.7 cm long, lanceolate, apex obtuse or acute. Umbel 3–10 flowered, pedicels erect, to .5 cm long. Flowers distylous. Calyx campanulate, somewhat farinose, obscurely ribbed, .4–.6 cm long, green or with purple striations, lobed about one third its length, teeth with capitate glands. Corolla white, throat yellow; tube .4–.7 cm long; limb .6–1 cm wide, lobes deeply cordate. Stamens ca. 1.5 mm long, anthers located toward the middle of the corolla tube.

Pollen 3-syncolpate. Stigma capitate, in pin plants located in upper third of corolla tube, positions reciprocal in thrum plants. Capsules not seen.

CHROMOSOME NUMBER. $n = 9$ (Idaho: Cholewa and Henderson, 1984).

HABITAT. Wet alkaline meadows.

DISTRIBUTION. Endemic to Idaho west of the Lemhi Range.

**Primula anvilensis** S. Kelso, Sys. Bot. 12: 9–13. 1987. Figure 1B.
*P. parvifolia sensu* Fernald (non Duby), Rhodora 30: 93. 1928; Hultén, Fl. Alaska and Yukon, Acta Univ. Lund 4: 1273. 1948. TYPE: U.S.A. ALASKA. Nome area: Anvil Mt., *Kelso 83-136* (HOLOTYPE: ALA!; ISOTYPES: CAN!, COLO!, NY!).

Plants slender, efarinose. Scape 2–10 (12.5) cm tall. Leaves bright green, cuneate or spathulate, including the petioles .5–1 (2) cm long, margins strongly denticulate near the apex; the blade .2–.4 cm wide, gradually narrowing onto a winged petiole .2–.4 cm long. Involucral bracts lanceolate, .2–.5 cm long, plane at the base. Umbel 1–5 (7) flowered; pedicels filiform, .5–1 cm long. Flowers distylous. Calyx efarinose, campanulate, obscurely ribbed, .2–.4 cm long, green or with purple striations, divided to one third its length, teeth lanceolate with capitate glands. Corolla white with a yellow throat; limb .5–.8 cm wide, emarginate; tube equal to the calyx or only slightly longer. Stamens .5–.75 mm long, anthers located in the lower third of the corolla tube in pin plants. Pollen 3-syncolpate. Stigma capitate, located in the upper third of the corolla tube in pin plants, positions reciprocal in thrum plants. Capsule cylindrical, .3–.5 cm long, .2–.3 cm in diam., strongly exserted from the calyx; seeds brown, strongly reticulate, .3 mm long.

CHROMOSOME NUMBER. $2n = 18$ (Nome: *Kelso 83-136*, at ALA).

HABITAT. Frost boils, late snowbeds, creek banks and gravel bars with calcareous substrates.

DISTRIBUTION. Endemic to and common on the Seward Peninsula, northwestern Alaska.

The species we now know as *Primula anvilensis* was first described by Fernald (1928), using the incorrect name *P. parvifolia.* The latter epithet came from a brief diagnosis of Duby, based on material collected by Langsdorff in 1805 from the southern Bering

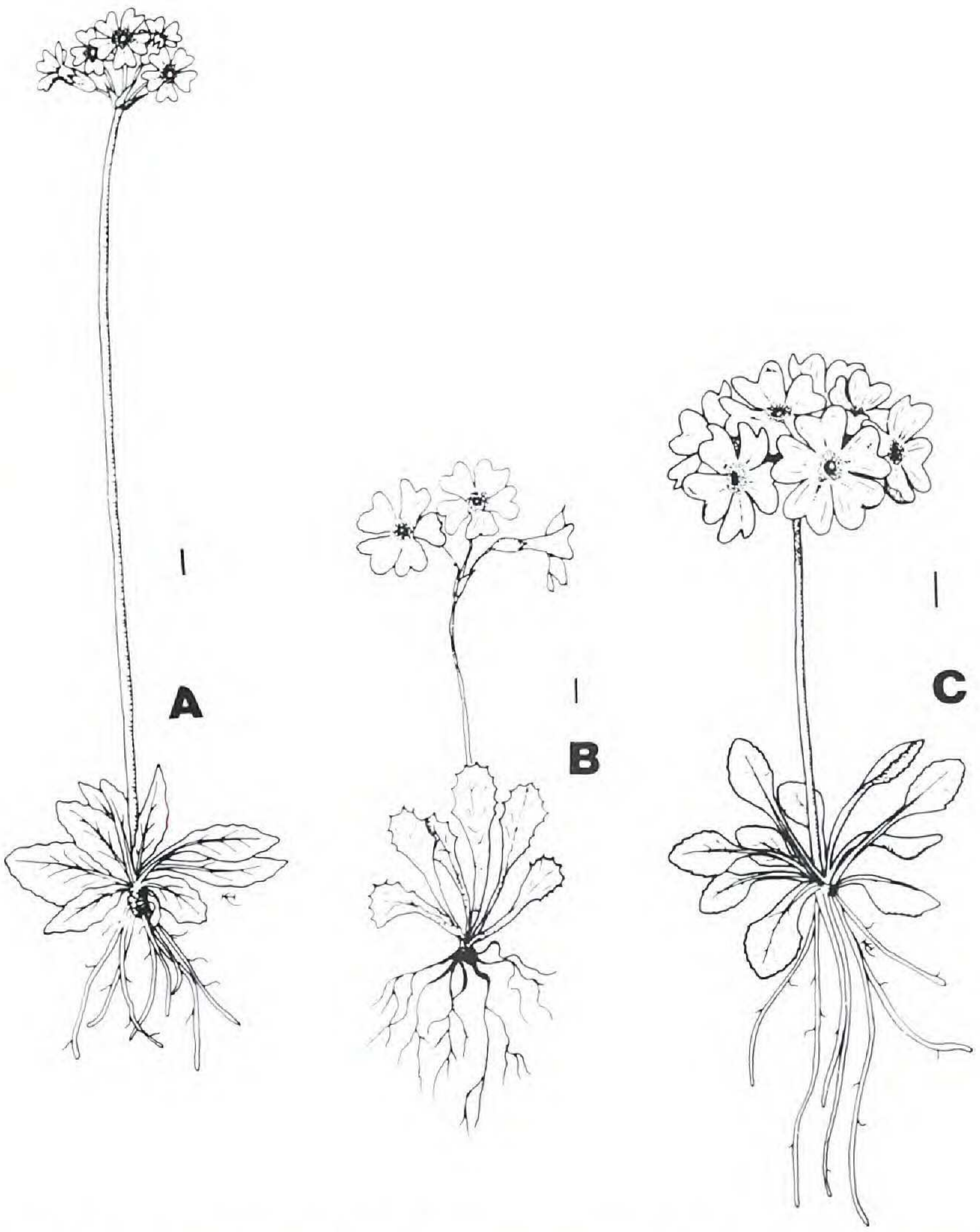

Figure 1. A. *Primula alcalina*, B. *P. anvilensis*, C. *P. borealis*. Bar equals 1 cm.

Sea region. These plants were given to Fischer at Leningrad, with duplicates sent to Kew and Edinburgh under the name *P. araboides* from herb. Fischer (Smith and Fletcher, 1943). When the name *P. parvifolia* was shown by Smith and Fletcher (1943) to be a synonym of *P. borealis*, the distinctive nature of the Seward Peninsula material was obscured in spite of Fernald's detailed description. It was not until recently that the Seward Peninsula material was separated from *P. borealis* by Kelso (1987) and given the name *P. anvilensis*.

*Primula anvilensis* is endemic to the Seward Peninsula of northwestern Alaska. While there are a number of plant taxa restricted to the Bering Strait region, *P. anvilensis* is unusual in having a wholly North American distribution.

**Primula borealis** Duby, Mem. Soc. Phys. d'Hist. Nat. Génève 10: 31. 1843; in DeCandolle, Prodromus 8: 43. 1844. Figure 1C. TYPE: U.S.A. ALASKA. Shishmaref, *Chamisso & Eschscholtz in 1816* (LECTOTYPE here designated: LE, photograph E!).

*Primula mistassinica sensu* Chamisso & Schlechtendal (*non* Michaux), Linnaea 1: 213–215. 1826.

*Primula parvifolia* Duby, in DeCandolle, Prodromus 8: 42. 1844. *Primula borealis* var. *parvifolia* (Duby) Pax, in Engler, Pflanzenreich, Primulaceae, 81. 1905. TYPE: "*Ad fretum Beering*" as *P. araboides, nomen nudum,* in herb. Fischer (HOLOTYPE: LE?; ISOTYPES: E!, K!, NY!).

*Primula tenuis* Small, Bull. Torr. Bot. Club 25: 320. 1898. TYPE: U.S.A. ALASKA. Pastolic, 25 Jun 1871, *Dall s.n.* (HOLOTYPE: NY!, photograph E!).

*Primula chamissonis* Busch, Fl. Sib. & Orient. Extrem. 4: 28. 1926. TYPE: U.S.A. ALASKA. Kotzebue, 1816–17, *Chamisso s.n.* (HOLOTYPE: LE, Photo GH!).

Plants growing in dense clusters or single, farinose in youth, becoming more or less efarinose in age. Scape (1) 2–10 cm tall. Leaves including petiole 1–2 (3.5) cm long, .1–.7 cm wide, spathulate, elliptical, or rhombic, margins crenate to remotely denticulate. Involucral bracts gibbous or saccate at base, involute above, .2–.5 cm long. Umbel (1) 3–8 (12) flowered. Pedicels .2–.8 cm long, erect or spreading but not capillary. Flowers distylous. Calyx campanulate, green or with purple striations, ca. .3 cm long, obscurely ribbed, divided up to ½ its length with lanceolate teeth covered with capitate glands. Corolla lavender, rarely white, throat yellow; tube .6–.8 cm long, at anthesis 1.5 times length of the calyx; limb (.8) 1–1.5 cm wide, lobes slightly or deeply emarginate. Stamens ca. 1 mm long, anthers located near middle of the corolla tube in pin plants. Pollen 3-syncolpate. Stigma capitate, in pin plants located at or just above the annulus. Positions reciprocal in thrum plants. Capsule cylindrical, .3–.6 cm long, .2–.3 cm in diam., strongly exserted from the calyx. Seeds strongly reticulate, ca. .3 mm long.

CHROMOSOME NUMBER. $2n = 36$ (Alaska: *Kelso 84-115, 83-292,* at ALA; Johnson and Packer, 1968; Northeast Siberia: Zhukova, 1965, 1966, 1982; Zhukova and Tikhonova, 1971; Zhukova et al., 1973). $2n = 18$ (Alaska: Thomas, 1951; Siberia: Zhukova, 1980; Zhukova and Petrovsky, 1980, q.v. *P. mistassinica*).

HABITAT. Coastal estuarine marshes.

DISTRIBUTION. In North America from the Bering Sea coast to Cape Bathurst in the Northwest Territories. Total range in Asia uncertain, but clearly present along the coast from the Chukotsk Peninsula to the Kolyma River.

In 1816–17, Chamisso and Eschscholtz travelled through the Bering Strait with the Kotzebue expedition, collecting at Unalaska, St. Lawrence Bay (Chukotka), St. Lawrence Island, and Shishmaref (then spelled Schischmareff). In a later enumeration of the plants from this expedition, Chamisso misidentified several specimens as *Primula mistassinica.* The formal description of *P. borealis* was not made by Duby until several decades later, based on the collections of Chamisso ("*in Americae occidentali-borealis sinubus schischmareff et Sancti Laurentii*"). Although Bunge is also listed as a collector of type material, this cannot be correct since he never visited the area. Duby was possibly referring to specimens from herb. Bunge, collected by Chamisso and Eschscholtz. It is appropriate, therefore, to designate the Chamisso material as the lectotype of *P. borealis.*

*Primula borealis* is variable in height, leaf morphology, and amount of farina, all of which are influenced by ecological and phenological factors. Dune populations contain individuals less than 2 cm in height, whereas individuals growing in more stable, nutrient-rich sites can attain over 10 cm. Leaf length increases over a growing season, and the amount of farina present appears to be related to phenology. Young leaves are heavily farinose, but later in the summer only a few traces of farina may remain.

Floral morphology is consistent in *Primula borealis.* The wide corolla limb, full symmetrical umbel, and short pedicels on top of a short scape make the plants appear top-heavy at anthesis. Individuals growing in environmentally stressed areas, however, often have depauperate umbels. The specimens described by Small as *P. tenuis* are typically of this growth form. In live material, the involucral bracts are consistently saccate or gibbous but this character may be difficult to detect in some herbarium material.

*Primula borealis* is always found in saline habitats. It can be sympatric with *P. nutans,* and herbarium sheets frequently contain both species. *Primula nutans* is easily distinguished from *P. borealis* by its ovate petiolate leaves and auriculate bracts.

The collection from the interior of the Yukon reported in Porsild (1966) and Porsild and Cody (1980) as *Primula borealis* was based on a misidentification of *P. mistassinica.* Because of insufficient specimens available for inspection, the range of *P. bo-*

*realis* in Siberia beyond the coast of Chukotka is unclear. Soviet literature (Yurtsev et al., 1979; Tolmatchev and Yurtsev, 1980; Kozhevnikov, 1981) reports the species as far west as the Lena River. However, the chromosome number attributed to *P. borealis* there (Zhukova and Petrovsky, 1980) is diploid rather than the tetraploid given in numerous other reports. The Eurasiatic taxon *P. farinosa* L. is a diploid and is found throughout northern Siberia, including the Lena River basin. It can resemble *P. borealis* and it is likely that there has been some confusion between the two species. Consequently, I hesitate to accept the conclusion of Smith and Fletcher (1943) that the Siberian *P. stricta* var. *jacutensis* Busch is entirely synonymous with *P. borealis.* They are certainly correct that it is not a form of *P. stricta.* However, I suspect that the specimens cited by Busch from the mountainous region along the Lena River, and the specimens identified as *P. borealis* with the diploid chromosome number reported by Zhukova and Petrovsky (1980) from the Anyui Mountains, should be allied with *P. farinosa* rather than with *P. borealis.*

South of the Chukotsk Peninsula, it is difficult to separate the range of the North Pacific species *Primula modesta s. lat.* from that of *P. borealis.* No recent systematic work has been done on the Asiatic members of sect. *Aleuritia,* but there is clear affinity between *P. borealis* and *P. modesta* in their large flowers, symmetrical umbels, and rhomboid leaves. *Primula modesta* is known to be diploid (Shimizu, 1982) and the other diploid chromosome counts reported for *P. borealis* in Siberia are from the mountains along the Sea of Ochotsk (Yurtsev et al., 1979), near the range of *P. modesta.* I suspect that the lower chromosome numbers attributed to *P. borealis* in this region are applicable instead to one of the varieties of *P. modesta.*

**Primula incana** M. E. Jones, Proc. Cal. Acad. Sci. 5: 706. 1895. Figure 2A. *P. farinosa* var. *incana* (M. E. Jones) Fernald, Rhodora 9: 16. 1907. *P. farinosa* subsp. *incana* (M. E. Jones) Smith and Forrest, Notes Roy. Bot. Garden Edinburgh 16: 24. 1928. TYPE: U.S.A. UTAH. Tropic, *Jones 5312* (HOLOTYPE: RSA!).

*Primula americana* Rydberg, Bull. Torrey Bot. Club 28: 500. 1901. TYPE: U.S.A. MONTANA. Deer Lodge, *Rydberg 2746* (HOLOTYPE: NY!).

Plants slender and heavily farinose, occasionally efarinose. Scape

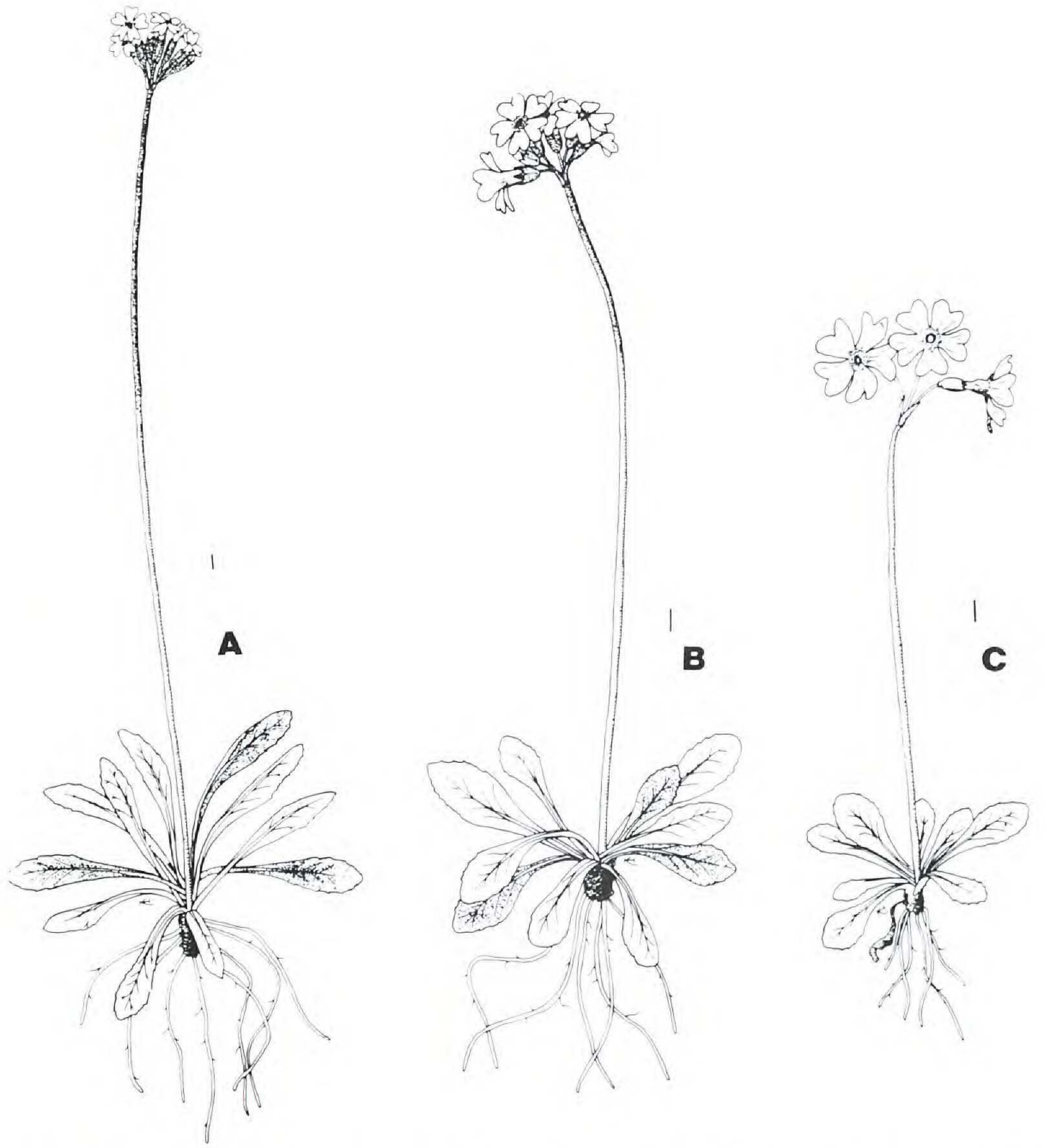

Figure 2. A. *Primula incana*, B. *P. laurentiana*, C. *P. mistassinica*. Bar equals 1 cm.

to 46 cm tall. Leaves elliptic or oblanceolate, including the petioles to 6 cm long, blade .3–1.6 cm wide, margins denticulate, blade gradually narrowing onto a broadly winged petiole. Involucral bracts oblong, densely covered with white farina, flat above, saccate or gibbous at the base, .5–1 cm long. Umbels capitate, (4) 7–19 flowered, pedicels .3–.9 cm long. Flowers homostylous. Calyx green, heavily farinose, cylindrical, obscurely ribbed, .4–.7 (1) cm long, divided up to one third its length by lanceolate teeth covered with capitate glands. Corolla lavender with yellow throat; limb .4–.8 cm wide, tube equal to or slightly longer than calyx, limb emarginate. Stamens ca. 1 mm long, located in upper portion of corolla tube. Pollen 4-syncolpate. Stigma capitate, located adjacent to anthers. Capsule cylindrical to slightly elliptical, .8–1.8 cm long, .2–.3 cm in diam. Seeds brown, reticulate, ca. .2 mm long.

CHROMOSOME NUMBER. $2n = 54$ (Alaska: *Kelso 83-350, 84-53, 84-91*; Yukon: *Kelso and Holmes 84-37,* all at ALA). $2n =$ ca. 50 (Colorado: *Wittmann and Wittmann 2542,* at ALA). $2n = 72$ (Colorado: Vogelmann, 1960).

HABITAT. Alkaline clay soil in river flood plains and open meadows.

DISTRIBUTION. Utah and Colorado north to Alaska.

*Primula incana* is a generally well-marked species with heavily farinose leaves, tall scape, and flat-tipped bracts subtending tight umbels of small homostylous flowers. Many northern collections have been misidentified as the smaller *P. stricta* because flowering begins when the scape is relatively short. Elongation of the scape continues throughout anthesis and pedicels lengthen as seeds ripen. Thus, the characteristic tight umbels do not persist beyond anthesis, and individuals in fruiting stage may be many times taller than those in early flowering stage. While most plants are heavily farinose, some individuals in otherwise farinose populations may be efarinose. *Primula incana* is most similar to *P. laurentiana.* The latter is distinguished by larger flowers, longer pedicels, broader, more denticulate leaves and involute rather than flat bracts.

A single octoploid count for *Primula incana* has been reported (Vogelmann, 1960) from a population in South Park, Colorado, but I have obtained a hexaploid count from the same locale. The consistency of chromosome number at the species level in sect. *Aleuritia,* the number of hexaploid counts for this species, and the complete lack of morphological or anatomical differences between northern specimens and the southern populations are evidence that the octoploid count may be in error and the species is consistently hexaploid.

**Primula laurentiana** Fernald, Rhodora 30: 68–72. 1928. Figure 2B. *P. farinosa* L. var. *macropoda* Fernald, Rhodora 9: 16. 1907. *P. mistassinica* Michx. var. *macropoda* (Fernald) Boivin, Nat. Can. 93: 644. 1966. TYPE: CANADA. QUEBEC. Le Bic, *Fernald and Collins 243* (HOLOTYPE: GH; ISOTYPE: MN!).

*Primula laurentiana* f. *chlorophylla* Fernald, Rhodora 30: 72. 1928. TYPE: CANADA. NEWFOUNDLAND. Dog Peninsula, St. Margaret Bay, *Fernald et al. 28913* (HOLOTYPE: GH!).

Plants usually heavily farinose, glabrous. Scape 10–30 (48) cm tall. Leaves including petiole 3–10 cm long, oblanceolate to spathulate, rounded or acute at the apex with crenate margins, blade .4–1.3 cm wide, gradually narrowing into winged petioles, densely farinose below with white or cream-colored farina. Involucral bracts saccate at base, involute above, .6–.8 cm long. Umbel 3–12 flowered; pedicels up to 1 cm long, elongating greatly in fruit. Flowers homostylous. Calyx campanulate to tubular, green, obscurely ribbed, .5–.8 cm long, divided up to ⅓ its length by lanceolate teeth, densely covered with capitate glands. Corolla lavender with a yellow throat, tube .6–.9 cm long, 1.5–2 times the length of the calyx at anthesis; limb to 1.6 cm wide, lobes to 0.7 cm wide, emarginate. Stamens ca. 1 mm long, anthers located adjacent to the stigma in the upper ⅓ of the corolla tube. Pollen 4-syncolpate. Capsule elliptical, up to 1.4 cm long, .3–.5 cm in diam., exserted from the calyx. Seeds brown, ca. .3 mm long, reticulate.

CHROMOSOME NUMBER. $2n = 72$ (unknown location: Bruun, 1938; Labrador and Quebec: Vogelmann, 1960; Quebec: Gervais and Cayouette, 1985). $2n = 54$ (Labrador: Vogelmann, 1960).

HABITAT. Open areas on limestone, along riverbanks.

DISTRIBUTION. Common on the Gaspé Peninsula of Quebec and in limestone regions of western Newfoundland, infrequent west to Hudson Bay and south to northeastern Maine.

*Primula laurentiana* is most similar to *P. incana* M. E. Jones. The latter species is also usually tall and heavily farinose, but has smaller flowers, flat bracts, a more western distribution, and is a hexaploid. While a single hexaploid count has been published for *P. laurentiana,* the number of other octoploid counts suggests that this may be erroneous, although further cytological investigations in Newfoundland would be helpful.

The efarinose form of *P. laurentiana* described by Fernald as f. *chlorophylla* is a common variant occurring throughout the range. Because efarinose individuals can be found in virtually all farinose populations, I do not believe they deserve taxonomic recognition.

**Primula mistassinica** Michaux, Fl. Bor.-Amer. 1: 124. 1803. Figure 2C. *P. farinosa* var. *mistassinica* (Michaux) Pax, Bot. Jahrb. Syst. 10: 200. 1889. *P. farinosa* subsp. *mistassinica* (Michaux) Pax and Knuth, Das Pflanzenreich 4(237): 85. 1905. *P. sibirica* var. *mistassinica* (Michaux) Kurtz, Bot. Jahrb. Syst. 19: 394. 1894.—*pro parte.* TYPE: CANADA. QUEBEC. Rivière des Goelands, Lake Mistassini. "*Ad locus mistassins Canadam inter et fretum Hudsonis,*" 1792, *Michaux s.n.* (HOLOTYPE: P).

*Primula intercedens* Fernald, Rhodora 30: 86–87. 1900. *P. mistassinica* var. *intercedens* (Fernald) Boivin, Nat. Canad. 93: 644. 1966. *P. mistassinica* f. *intercedens* (Fernald) J. Cayouette, Nat. Canad. 111: 443–445. 1984. TYPE: *P. farinosa sensu* Nuttall, Gen. 1: 119. 1818, "calcareous gravel shores of the islands of Lake Huron around Michilimakinak, Bois Blanc, and St. Helena in the outlet of Lake Michigan," and *P. farinosa* var. *americana* Torrey, Fl. North. & Midl. U.S. 1: 213. 1824, "shores of Lake Huron, Lake Michigan, etc. *Douglass* and *Nuttall*" (LECTOTYPE here designated: PH!, *Douglass s.n.*, Lake Huron, ex herb. Schweinitz).

*Primula mistassinica* var. *noveboracensis* Fernald, Rhodora 30: 19. 1928. TYPE: U.S.A. NEW YORK. Triphammer Falls, Fall Creek, Ithaca, *Eames 4804* (HOLOTYPE: GH!).

*P. maccalliana* Wiegand, Bull. Torr. Bot. Club 27: 389. 1900. TYPE: CANADA. ALBERTA. Banff. *Maccalla 2433* (HOLOTYPE: CU; ISOTYPE: K!).

Plants usually efarinose, glabrous, sometimes with traces of farina on vegetative parts. Scape 5–15 cm tall. Leaves including the petiole .5–7 cm long, spathulate or elliptical, margins widely denticulate to almost entire; blade .2–1.6 cm wide, gradually narrowing to winged petiole. Involucral bracts lanceolate, plane at base, .3–.5 cm long, involute above, acute or somewhat obtuse at the tip. Umbel 1–5 (10) flowered. Pedicels .5–2.0 cm long, capillary. Flowers distylous. Calyx green or with purple striations, campanulate, obscurely ribbed, .3–.5 cm long, divided up to ½ by lanceolate teeth sparsely covered with capitate glands. Corolla lavender, sometimes white; throat usually yellow, rarely lavender; tube .5–.8 cm long, at anthesis 1.5–2 times the length of the calyx; limb .8–1.4 cm wide, lobes emarginate. Stamens ca. 1 mm long, anthers located in pin plants in bottom third of corolla tube. Pollen 3-syncolpate. Stigmas capitate, located in pin plants in upper third of corolla tube, positions reciprocal in thrum plants. Capsule cylindrical to elliptical, .3–.6 cm long, .2–.3 cm in diam., seeds ca. .3 mm long, reticulate.

CHROMOSOME NUMBER. $2n = 18$ (Yukon: *Kelso and Holmes 84-15,* at ALA; Michigan, New York, Nova Scotia, Quebec: Vogelmann, Ph.D. dissertation, Univ. of Michigan, 1956, 1960).

HABITAT. Open meadows and riverbanks, lakeshores, and around hot springs, in the southern portion of the range on cool, wet, north-facing slopes and cliff faces; calcareous substrates.

DISTRIBUTION. Across boreal America from Alaska to Newfoundland, south to northern Vermont, New York, Illinois, Michigan, and Minnesota.

*Primula mistassinica* is one of the most polymorphic North American species in sect. *Aleuritia.* Previous authors (cf. Fernald, 1907, 1928; Vogelmann, *loc. cit.*) have recognized several infraspecific taxa. While *P. mistassinica* varies in size, leaf morphology, and the amount of farina, it is consistent in habit, chromosome number, and floral morphology. The infraspecific taxa lack clear geographic coherence, intermediate forms are abundant, and it is often difficult to assign material to varietal level. Among the taxa recognized by previous authors, individuals belonging to var. *intercedens* (distinguished by the presence of yellow farina) are particularly abundant around the Great Lakes. However, individuals with variable amounts of farina can be found throughout the range of *P. mistassinica.* Similarly, individuals belonging to var. *noveboracensis* (distinguished by smaller flowers and lack of a yellow eye) are abundant in Newfoundland and in the Northwest, but can also be found throughout the range. For these reasons, I believe *P. mistassinica* is best treated as a single polymorphic species without infraspecific designations.

The range of *Primula mistassinica* is generally sympatric with the boreal forest of North America. In the northwestern portion of the range, *P. mistassinica* becomes increasingly rare and is recognized as threatened or endangered in several Canadian provinces. In northwestern Canada and Alaska it is better documented by herbarium specimens than previously believed, although it should still be considered rare. Many of the specimens from the continental Northwest Territories and Yukon initially identified as the homostylous *P. stricta* are actually the distylous *P. mistassinica.* Two populations from the interior Yukon (*Spetzman 311, 312,* DAO!) identified by Porsild (1966) as *P. borealis* are also *P. mistassinica. Primula mistassinica* differs from *P. borealis* in its more slender habit, plane involucral bracts, and fewer-flowered

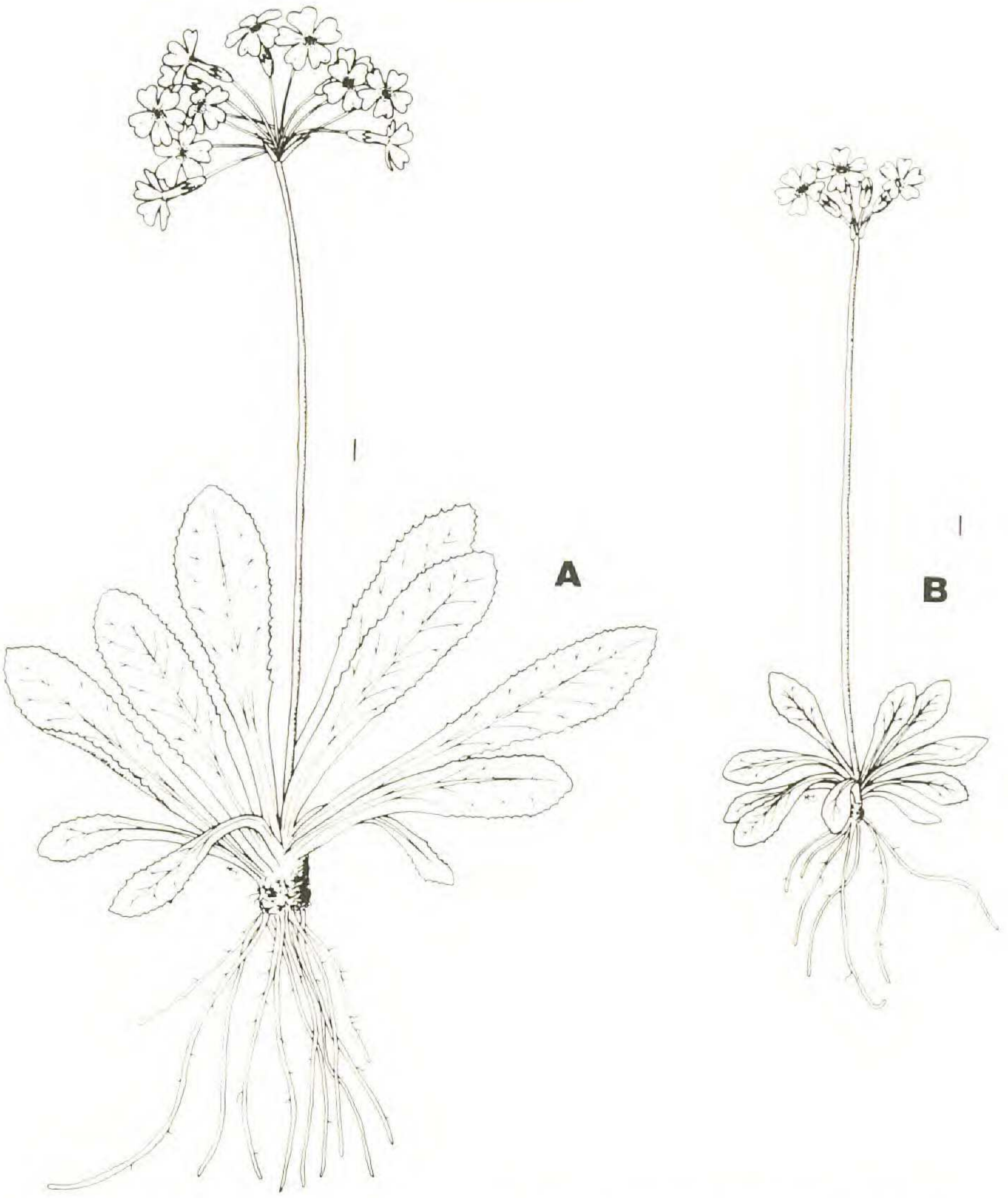

Figure 3. A. *Primula specuicola*, B. *P. stricta*. Bar equals 1 cm.

umbel on longer pedicels, as well as by the lower chromosome number.

**Primula specuicola** Rydberg, Bull. Torrey Bot. Club 40: 461–462. 1913. Figure 3A. TYPE: U.S.A. UTAH. San Juan River, near Bluff (HOLOTYPE: *Rydberg 9882*, NY!).

*Primula hunnewellii* Fernald, Rhodora 36: 117. 1934. TYPE: U.S.A. ARIZONA. Coconino County, north rim of the Grand Canyon (HOLOTYPE: *Hunnewell 10883* in Hunnewell Herbarium; ISOTYPE: GH!).

Plants heavily farinose. Scape to 25 cm tall. Leaves spathulate, including petioles to 13 cm long, blade to 2 cm wide, margins strongly sinuate-dentate, blade gradually narrowing to a broadly winged petiole. Involucral bracts lanceolate, plane at base and involute above, a broadly winged petiole. Involucral bracts lanceolate, plane at base and involute above, .5–1 cm long. Umbels loose, (6) 10–25 flowered, pedicels ascending, 1–3 cm long. Flowers distylous. Calyx green, campanulate, obscurely ribbed, .3–.5 cm long, divided to ⅓ its length by lanceolate teeth covered with capitate glands. Corolla violet, with a yellow throat; limb 1–1.6 cm broad, tube .8–1 cm long, twice the length of the calyx. Anthers ca. 1.5 mm long, stamens located in the middle of the corolla tube in pin plants. Pollen 3-syncolpate. Stigma capitate, located in upper ⅓ of corolla tube in pin plants, positions of anthers and stigma reciprocal in thrum plants. Capsule elliptical, .3–.5 cm long, ca. .3 cm in diam. Seeds ca. .5 mm long, reticulate.

CHROMOSOME NUMBER. $2n = 18$ (Vogelmann, 1960).

HABITAT. Moist seepage areas on carbonate canyon walls along the Colorado River and its tributaries.

DISTRIBUTION. Southern Utah and northern Arizona.

*Primula specuicola* is a distinctive species with large corollas, long pedicels, and long, sharply dentate, farinose leaves. A few specimens with short pedicels superficially resemble *P. incana* but the latter is distinguished by its smaller, homostylous flowers and longer capsules as well as its higher chromosome number.

A specimen from the Grand Canyon with a more exserted capsule than in the type material from Utah was given the name *Primula hunnewellii* by Fernald (1934). The Arizona plant resembles the type of *P. specuicola* in all other aspects of morphology, cytology, and ecology, and I believe that *P. hunnewellii* is merely a local variant of *P. specuicola.*

**Primula stricta** Hornemann, in Oeder, Flora Danicae 8(24): t. 1385. 1810. Figure 3B. *P. hornemanniana* Lehm. Monogr. Gen. Prim. 55. 1817—*pro parte.* TYPE: NORWAY. Tolgen and Roraas, *Hornemann s.n.* (HOLOTYPE: C, microfiche ALA!). *P. farinosa* var. *groenlandica* Pax in Engler, Pflanzenr. Primulaceae 84. 1905.—*pro parte.*

Plants efarinose or sparingly farinose. Scape 8–15 (18.5) cm tall. Leaves including petiole 1–6 cm long, oblanceolate to spathulate, margins slightly denticulate to almost entire, blade .3–1.1 cm broad, gradually narrowing onto winged petioles. Involucral bracts lanceolate, acute at the tip, saccate at base, involute above,

.6–1.0 cm long. Umbel 2–9 flowered, pedicels .1–.8 cm long, elongating slightly in fruit. Flowers homostylous. Calyx green or with purple striations, campanulate, obscurely ribbed, .4–.6 cm long, divided up to ⅓ by lanceolate teeth, with capitate glands on the margins, somewhat white farinose on the inner surface. Corolla tube .4–.7 cm long, slightly exserted from calyx at anthesis, limb .5–.8 cm wide, lobes slightly emarginate. Stigmas capitate, located just below the annulus. Stamens ca. .75 mm long, anthers adjacent to stigma. Pollen 5-syncolpate. Capsules ovoid-elliptical, .5–.7 cm long, .3–.4 cm in diam. Seeds strongly reticulate, ca. .3 mm long.

CHROMOSOME NUMBER. $2n = 126$ (unknown location: Bruun, 1930; Iceland: Löve and Löve, 1956; Manitoba: Löve and Ritchie, 1966). $2n > 90$ (Norway: Laane, 1967).

HABITAT. Coastal regions including marshes, stable dunes and beach ridges, more rare inland along rivers.

DISTRIBUTION. In North America throughout the southern islands of the Canadian Arctic Archipelago and Hudson Bay region, east through Greenland and Scandinavia to Novaya Zemlya.

The arctic species *Primula stricta* was originally described and illustrated by Hornemann from specimens collected in Norway. Its nature was confused, however, by Lehmann's use of the name *P. hornemanniana* for the same material, coupled with his description of the taxon based on what he erroneously thought was additional material from the Tyrol. This material was probably *P. farinosa* L., and thus the description and illustration in Lehmann's monograph refer to a chimera of *P. stricta* and *P. farinosa*. *Primula stricta* is not found in the Alps, and Hornemann's original name and description are correct for the species as we now understand it.

In its most typical form, *Primula stricta* is a short plant with capitate umbels, small emarginate corolla lobes, and broadly elliptical capsules barely longer than the calyx. Although height and number of flowers can vary, the morphology of the species remains generally consistent across the range in the Canadian and European Arctic. This consistency in *P. stricta,* however, has been obscured in North America by confusion with *P. incana.*

While some of the smaller forms of *Primula incana* resemble *P. stricta,* the typical forms are easy to distinguish. *Primula stricta* is less than one third the height of *P. incana,* lacks the dense farina of the latter except on the inner surface of the calyx, and has involute rather than flat-tipped involucral bracts. *Primula stricta* also has broader and shorter capsules than *P. incana,* and there are cytological differences between the two species: *P. stricta* is 14-ploid ($2n = 126$) and *P. incana* is a hexaploid ($2n = 54$).

In western North America, *Primula stricta* has been erroneously reported in the Yukon Territory and Alaska (Hultén, 1968; Porsild, 1966; Scoggan, 1979). Most of the records west of the Mackenzie Basin are based on misidentified specimens of *P. incana.* The confusion of the two taxa here is understandable, since in the interior of the Yukon, particularly in the saline clay pans around Kluane Lake, *P. incana* has a small efarinose form with depauperate umbels very similar to *P. stricta.* When transplanted to gardens in Fairbanks, these plants regained the tall farinose appearance typical of *P. incana.* Chromosome counts confirm that the Yukon populations are *P. incana* and not *P. stricta.*

In Alaska, Hultén (1948, 1968) reported *Primula stricta* in the interior, on the Seward Peninsula and on the arctic seacoast. These records are also based on misidentifications. The Seward Peninsula specimens are *P. anvilensis* (e.g., *Hutchinson 313-318, 313-331,* E!, K!), on the arctic coast they are *P. borealis* (e.g., *Johansen 265,* CAN!), and in the interior of Alaska they are *P. incana* (Copper Center: *Heideman 46,* US!). The specimens of *P. stricta* cited from the Yukon by Hultén (Five Finger Rapids: *Tarleton 78*; Lewes River: *Gorman 1052,* both at US!) are also *P. incana.*

## **Primula** sect. **Armerina**

**Primula** sect. **Armerina** Lindley, Edward's Bot. Reg. 32: t. 31. 1846. TYPE: *P. involucrata* Wallich.

Section *Farinosae* subsection *sibirica* Bruun, Symb. Bot. Upsal. 1: 67. 1932. TYPE: *P. sibirica* Jacquin.

Plants efarinose but with jointed hairs, sometimes rhizomatous. Leaves with revolute vernation, distinctly petiolate on slender, elongate petioles; blades entire or slightly undulate, glabrous. Inflorescence a simple umbel subtended by involucral bracts that are saccate and usually conspicuously auriculate at base; pedicels flexuous. Corolla lilac, pink, or white, lobes notched or cleft. Capsules narrowly cylindrical. Chromosome base number $x = 11$.

Schwarz (1968) divided section *Armerina* into two subsections: *Armerina* (including *Primula nutans*) and *Chamaecome* (including *P. egaliksensis*). He distinguished the latter section by its persistent rhizomes, in contrast to subsection *Armerina* with rhizomes lasting only a single growing season. At best this distinction seems weak, and at least in Alaska, completely false. Consequently, I do not follow the divisions of Schwarz, and treat all the species related to *P. nutans* as members of a single section.

### KEY TO SECTION *ARMERINA* IN NORTH AMERICA

Involucral bracts distinctly auriculate at the base; flowers 8 mm or more in diameter .......................... *P. nutans*

Involucral bracts saccate at base but not auriculate; flowers less than 8 mm in diameter .................... *P. egaliksensis*

**Primula egaliksensis** Wormskjold *ex* Hornem., Fl. Danicae 9: 2, t. 1511. 1816. Figure 4B. TYPE: GREENLAND. Igaliko, 1813, *Wormskjold s.n.* (HOLOTYPE: C; ISOTYPE: E!).

*P. stricta* var. *groenlandica* Warming, Kongl. Svenska Vetenskapsakad. Handl. 12: 21. 1887. *P. farinosa* var. *groenlandica* (Warming) Pax, in Engler, Das Pflanzenreich, Primulaceae 84. 1905.—*pro parte. P. groenlandica* (Warming) Balfour, J. Royal Hort. Society 34: 182. 1913. *P. egaliksensis* f. *violacea* Fernald, Rhodora 30: 98. 1928. TYPE: GREENLAND. Itivnek, Holsteinborg District, 13 Jul 1884, *Warming & Holm s.n.* (HOLOTYPE: C; ISOTYPES: GH!, K!).

*P. sibirica* Hooker, Fl. Bor. Am. 2: 121. 1838.—*pro parte. P. sibirica* var. *minor* Duby, in DeCandolle, Prodromus 8: 43. 1844.

Plants slender, completely efarinose. Scape 4–12.5 cm tall. Leaves distinctly pedicellate, including the petiole 1.5–5.5 cm long, blade elliptical, to .9 cm wide, .7–2.5 cm long, margins entire, obscurely undulate or slightly denticulate in age. Involucral bracts lanceolate, to .6 cm long, distinctly saccate but not auriculate at the base, somewhat involute above. Umbel 1–3 (6) flowered, pedicels pendant, .2–.9 cm long. Flowers homostylous. Calyx cylindrical, obscurely ribbed, .4–.6 cm long, green or with purple stripes, divided to ⅓ by teeth with glandular cilia on the margins. Corolla white or lavender, throat yellow; limb .6–.8 cm wide, slightly emarginate, tube .6–.8 cm long, equal to or slightly exserted from the calyx. Stamens ca. .75 mm long, anthers located adjacent to stigmas in upper one third of corolla tube. Pollen

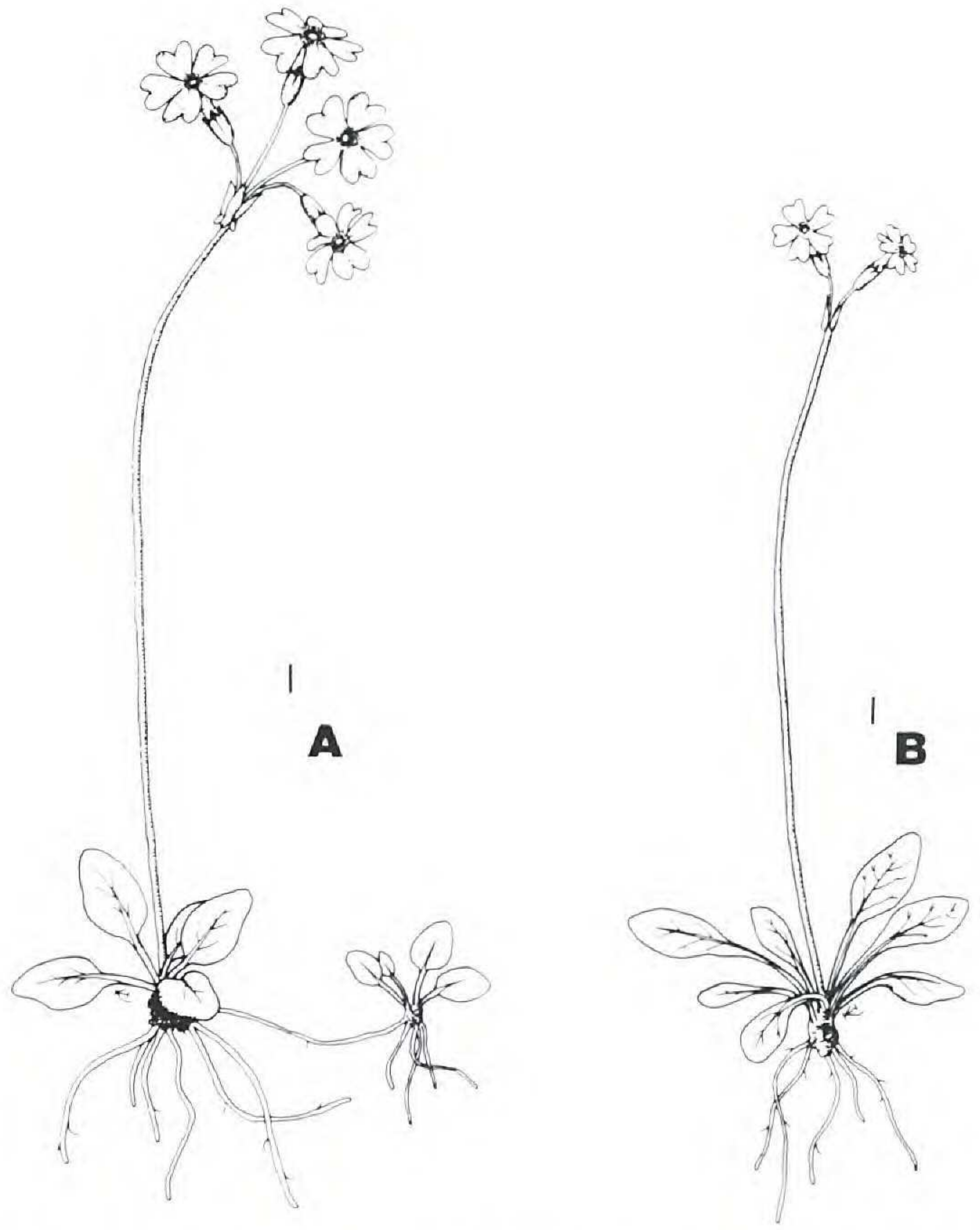

Figure 4. A. *Primula nutans*, B. *P. egaliksensis*. Bar equals 1 cm.

5-syncolpate. Stigma cylindrical. Capsule narrowly cylindrical, up to 1.2 cm long, ca. .1 cm in diam. Seeds green to light brown, obscurely reticulate, to .3 mm long.

CHROMOSOME NUMBER. $2n = 36$ (Alaska: *Kelso 85-10*, *Parker 2007*, both at ALA; Colorado: Löve et al., 1971; Greenland: Jørgenson et al., 1958). $2n =$ ca. 36 (Alaska: Johnson and Packer, 1968). $2n = 40$ (Northeast Siberia: Zhukova et al., 1973; Zhukova, 1982). $2n =$ ca. 40 (Labrador: Hedburg, 1967).

HABITAT. Damp silt along streambanks.

DISTRIBUTION. Across North America from Alaska to Greenland, known in the south from disjunct locations in Colorado and northwestern Wyoming; in Asia, known from the Chukotsk Peninsula.

*Primula egaliksensis* is easily distinguished by its inflorescence of 1 or 2 small homostylous flowers and its elliptical efarinose leaves. Both white and violet flowers are equally common and adjacent populations can occur. This dimorphism confused

Warming who allied the lilac form in Greenland to *P. stricta* rather than to the white-flowered taxon described by Wormskjold. This error was corrected by Fernald who examined Warming's material, removed it from *P. stricta,* and renamed it as a color variant of *P. egaliksensis.*

*Primula egaliksensis* has a wide geographic range but it is not locally abundant. Because of the small flowers and generally short stature, individual plants are inconspicuous even during the brief flowering period.

**Primula nutans** Georgi, Bemerk. Russ. Reich 1: 200. 1775. Figure 4A. TYPE: *J. G. Gmelin,* Fl. Sib. 4: t. 46. 1769. "*Ab Ob fluvio ad transbaicalensis usque ad regiones*" (HOLOTYPE: LE?).

*P. sibirica* Jacquin, Misc. Austr. 1: 161. 1778. Based on the same type as *P. nutans.*

Plants slender, efarinose, sometimes rhizomatous. Scape 5–20 cm tall. Leaves distinctly pedicellate, including petioles to 3 cm long; blade ovate to slightly elliptical, to 2 cm wide, 1–2 cm long, margins entire. Involucral bracts .4–.6 cm long, oblong, obtuse at the tip, saccate and prominently auriculate at the base. Umbel 2–4 flowered; pedicels nodding, 3 times the length of the bracts. Flowers distylous. Calyx cylindrical, .4–.7 cm long, distinctly ribbed, divided to ¼ its length by obtuse to somewhat acute teeth, with prominent ciliolate glands on the margins. Corolla violet with a yellow throat, tube .7–1 cm long, strongly exserted from the calyx in North American specimens; limb .9–2 cm wide, lobes cordate. Stamens 1.5–2 mm long, located in middle of corolla tube in pin plants and near top of corolla tube in thrum plants. Pollen 6-stephanocolpate. Stigma cylindrical, located in pin plants slightly above the annulus of corolla tube, and in thrum plants near middle of tube. Capsules narrowly cylindrical, to 1.4 cm long, .2–.4 cm in diam. Seeds light brown, ca. .4 mm long, rounded, reticulate.

CHROMOSOME NUMBER. $2n = 22$ (Alaska: *Kelso 84-05,* at ALA; Yukon: *Kelso and Holmes 84-21,* at ALA; Kamchatka: Sokolovskaya, 1968; Northeast Siberia: Zhukova et al., 1973; Norway: Engelskon, 1979; Borgen and Elven, 1983). $2n = 20$ (Mongolia: Hanelt, 1973; Lake Baikal, Siberia: Belaeva and Siplivinsky, 1975).

HABITAT. Salt marshes and estuaries along the coast, inland in sloughs and river flood plains.

DISTRIBUTION. Fennoscandia across northern and central Asia, coastal Alaska, rare in the interior of Alaska and the Yukon.

Until recently, *Primula nutans* has been known as *P. sibirica* Jacq. By the rules of the International Code of Botanical Nomenclature, the name *P. nutans* must be used because it antedates Jacquin's name by three years. Both Georgi and Jacquin used an unnamed Siberian primula (Gmelin, 1769) as the basis for their species. Jacquin apparently was not aware of Georgi's treatment when he named it *P. sibirica. Primula sibirica* was used by Duby (1844) in his monograph of the genus as the name *P. nutans* slipped into obscurity. Smith and Fletcher (1943) were aware of Georgi's treatment and listed *P. nutans* as a synonym of *P. sibirica,* but gave a later and erroneous date of publication (1797). Since the true date of publication of the name *P. nutans* is 1775, it takes precedence over *P. sibirica,* published in 1778. *Primula nutans* Georgi predates *P. nutans* Delavey, from China (section *Soldanelloides* Pax) which now becomes *P. flaccida* Balakr.

Although *Primula nutans* is geographically widespread, it is morphologically consistent. The only significant variation is in the relative lengths of calyx and corolla tube. Specimens from Fennoscandia have a corolla tube only slightly longer than the calyx; in Asiatic and North American specimens the corolla tube is twice the length of the calyx. The Scandinavian taxon is now treated as *P. nutans* subsp. *finnmarchia* (Jacquin) A. Löve & D. Löve (Löve and Löve, 1961; Mäkinen and Mäkinen, 1964).

In western Alaska *Primula nutans* is commonly found in estuarine marshes. It can be sympatric with *P. borealis* and the two species are often found mixed on herbarium sheets. *P. nutans* is easily distinguished from *P. borealis* by its ovate pedicellate leaves and auriculate bracts. It blooms approximately two weeks later than *P. borealis,* and unlike the latter, tolerates continually saturated soil.

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